DISCUSSING A MYTH: BIOMECHANICAL COMPARISONS BETWEEN *DINODONTOSAURUS* (SYNAPSIDA, DICYNODONTIA) AND EXTINCT GROUND SLOTHS [1]

(With 5 figures)

LEONARDO MORATO [2, 3]
CESAR LEANDRO SCHULTZ [2]
CRISTINA VEGA-DIAS [4]
FÁBIO PINTO DA SILVA [5, 6]
WILSON KINDLEIN JR. [5]

ABSTRACT: Dicynodonts possess a mosaic of features that includes the development of a differentiated posture in some genera: while the forelimbs remain abducted, in a sprawling posture, the hind limbs became fully improved. In the lack of modern analogues, comparisons with extinct ground sloths lead some authors to proposals of a bipedal posture, only facultative, which could enable the animal to rise on the hind limbs to reach higher vegetation. To test this hypothesis, some biomechanical aspects required to a bipedal posture were analyzed, regarding to specimens of the genus *Dinodontosaurus*, a medium-sized dicynodont from the Middle Triassic of Rio Grande do Sul State, Brazil. From observations of general morphology, location of the center of mass, estimation of moments of resistance of the vertebral column, and calculation of indicators of athletic abilities, we conclude that, at least in what concerns *Dinodontosaurus*, there are no evidences to support the morphofunctional analogies with the ground sloths.

Key words: Synapsida. Dicynodontia. *Dinodontosaurus*. Ground sloths.

RESUMO: Discutindo um mito: comparações biomecânicas entre Dinodontosaurus (Synapsida, Dicynodontia) e preguiças terrícolas extintas.

Dicinodontes possuem um mosaico de características que incluem o desenvolvimento de uma postura diferenciada em alguns gêneros: enquanto os membros anteriores permanecem abduzidos, em uma postura esparramada, os posteriores se tornam totalmente eretos. Na falta de análogos modernos, comparações com preguiças terrícolas extintas levaram alguns autores a propor uma postura bípede, ao menos facultativa, que permitiria ao animal erguer-se nas patas traseiras e alcançar vegetação mais elevada. Para testar essa hipótese, foram abordados vários aspectos biomecânicos envolvidos na postura bípede, aplicados em espécimes do gênero *Dinodontosaurus*, um dicinodonte de porte médio do Mesotriássico do estado do Rio Grande do Sul, Brasil. Através de observações morfológicas gerais, localização do centro de massa, estimativa de momentos de resistência da coluna vertebral e cálculo de índices de capacidade atlética para os membros, conclui-se que, ao menos no que concerne a *Dinodontosaurus*, não há evidências que apóiem as analogias morfo-funcionais com as preguiças terrícolas.

Palavras-chave: Synapsida. Dicynodontia. *Dinodontosaurus*. Preguiças terrícolas.

INTRODUCTION

The Dicynodontia comprises an extinct lineage of synapsids, originated in Late Permian and probably disappeared at the end of the Triassic, that developed into dominant primary consumers worldwide at least in two separate moments. Among a mosaic of peculiar features presented by them, we can enumerate: extreme dental reduction, presenting in most taxa only a pair of superior caniniform tusks, while the pre-maxilla and the anterior part of the dentary normally adopt the shape of a beak, being probably covered by a horny process (several forms during the Triassic lost the dentition completely, presenting just

caniform processes over the maxilla); the jaw articulation, which permits propalinal motion, is recorded even in basal forms through tooth striation (RYBCZYNSKI & REISZ, 2001), indicating the possibility of some oral food processing; broad anterior and posterior paws, of equal dimensions; fore and hind limbs plesiomorphically adducted and disposed laterally, but presenting considerable variation in orientation among later dicynodont taxa (RAY & CHINSAMY, 2003), in which the anterior limb can dispose closer to a parasagittal plane, but remaining adducted, while the hind limbs became fully abducted; and a barrel-shaped trunk, in some forms becoming very robust. Several taxa can also present some extend of cranial ornamentation, with thick and sculptured rostral regions, probably covered at some extend by horny sheets, indicated by the presence of nutrient foramina (MORATO *et al.*, 2005).

The lack of modern analogues to some of these characters presents difficulties to interpretations in functional basis. Nonetheless, to comprehend the success of Dicynodontia during their time span, it is necessary to investigate their adaptations to withstand in their habitat. This success is generally credited to their food-processing capabilities (CROMPTON & HOTTON III, 1967; COX, 1998), associated to their ecological flexibility (HOTTON III, 1986; RAYNER, 1992); in that topic, an increasing mobility in the hind limb could also deserve some attention (KING, 1981; FRÖBISCH, 2003).

HOTTON III (1986) describes the general dicynodont body form as "roughly comparable to that of such robust mammals as beavers (*Castor*) and New World badgers (*Taxidea*)", but with robust limbs. Dicynodonts lack the same specific adaptations as badgers or beavers for their burrowing lifestyles, although fossorial capabilities in several degrees were proposed, particularly in small Permian forms (*e.g.*, CLUVER, 1978; RAY & CHINSAMY, 2003).

COX's (1965) classification of triassic dicynodonts, particularly in respect to the families Kannemeyeriidae and Stahleckeriidae, takes in account some comparative proposals. He noticed among other characters that some forms present narrow beaks, while others have broad and robust beaks; similar differentiation was observed in the muzzle shape of rhinoceroses, distinguishing browsers, with pointed and prehensile lips and straight oriented occiputs in relation to the palate, of the grazers, with broad lips and tapering occiputs. However, as Cox himself observed, comparisons of feeding habits between them are not straight

forward, as the dicynodonts with narrow-shaped beaks possessed tapering occiputs, while in the broad-shaped forms, the occiput is vertical. Other attempt of comparisons in size and body form were made by CRUICKSHANK (1978), with modern Suidae, in which sloping occiputs were found in animals feeding close to the ground, as selective grazers, while upright occiputs are found in browsers and omnivorous forms. Although this seems to fit better with the dicynodont skull morphology, CRUICKSHANK (1978) is careful to extend these comparisons, as the suids in discussion are relatively more active animals, and their feeding behaviors transferred for the dicynodonts would ignore the available vegetation above the head heights of these animals.

Finally, the analysis of the morphology of extinct ground sloths (Xenarthra: Tardigrada) lead CRUICKSHANK (1978) to propose several inferences about feeding habits in dicynodonts, including the possibility of a bipedal posture, only facultative, for the animal to rise over the hind limbs and reach higher vegetation. The comparisons described by CRUICKSHANK (1978) refer more to the general external morphology, with emphasis in post-cranium, specially to the broad pelvic girdle, with high number of sacral vertebrae (some dicynodonts present up to 6), and the shape of the femur, which is transversally expanded, as well as other appendicular bones. Cruickshank thus could find a reason for the apparent dichotomy that developed in the limbs, with the hind ones becoming fully erect, with higher mobility in relation to the plesiomorphic pattern, and apparently under-used in respect to the restrictions imposed by the forelimbs, in a primitive sprawling posture (VEGA-DIAS & SCHULTZ, 2004).

These last comparisons, however, never were tested in a biomechanical basis. Here, a first attempt of biomechanical reconstruction is made, investigating several aspects involved in the bipedal or quadrupedal posture in a dicynodont species.

MATERIAL AND METHODS

Among dicynodont fossils collected in the Rio Grande do Sul State, the most complete and abundant remains belong to the genus *Dinodontosaurus* Romer, 1943 (Fig.1), a medium sized animal with up to 1.8m in length, from the Middle Triassic Santa Maria Formation. The paleovertebrate sector of the Universidade Federal do Rio Grande do Sul (UFRGS/PV) counts with fairly complete skeletons of ten juvenile individuals

(UFRGS/PV0111T-UFRGS/PV0120T) and one adult (UFRGS/PV0121T) attributed to this taxon, in which it was made the bulk of the following measurements and analyses. Additional material, for further comparisons, used mainly in the skeletal reconstructions, included well preserved skulls and partial skeletons, found in the collections of the Museu de Ciências e Tecnologia of the Pontifícia Universidade Católica do Rio Grande do Sul, in Porto Alegre, and of the Museu Municipal Guido Borgomanero, in Mata (RS).

A fundamental variable for a series of biomechanical analyses is the mass of the animal, which can be estimated from the volume of scale models. For the confection of the models, it was first effectuated skeletal reconstructions and accurate morphological restorations, trying to minimize the errors of the mass estimative. The restoration of soft tissues is also important subsequently, for the understanding of muscular action and for the interpretation of rest posture for the dicynodonts.

The volume of the model can be obtained through immersion in water, utilization of sand (COLBERT, 1962), or approximated from its lateral and dorso-ventral silhouettes. This last principle is utilized by the software PaleoMass (MOTANI, 2001), available at the World Wide Web, and was used here for the adult *Dinodontosaurus*. As the models were constructed in unfired water-based potter's clay, water could dissolve the model, and the use of sand is time-consuming and the results are also approximate. For the juvenile individuals, the clay model was digitalized through a laser 3D-scanner, and the volume of the digital model was calculated from the CAD (Computer Aided Drafting) software Rhinoceros® (trademark of Robert McNeel & Associates), after its conversion to non-uniform rational Bézier splines (NURBS) surfaces. With the volumes, the mean density for terrestrial vertebrates used for calculation of the mass was $1.0g/cm^3$, according to ALEXANDER (1985).

From the clay models, the center of mass can be located through the suspension by wires (Fig.2), in two positions, presuming that it is located in a point at the sagittal plane (ALEXANDER, 1985). Knowing the center of mass, it is also possible to estimate the distribution of corporal mass supported by each limb (FARIÑA, 2001) (Fig.2). For the digital model, the center of the volume could also be located with the software Rhinoceros (Fig.3), corroborating the location got from the real models.

SLIJPER (1946) argues that the moments of resistance for the vertebral column can be estimated only from dimensions of breadth and height of vertebral centra, using their posterior border for measurements. The resulting data can be plotted in a line graphic, in which the abscissas axis gives the position of the vertebra in the column, by its number, while the product of the breadth by the height at the square (bh^2) is plotted in the ordinates axis.
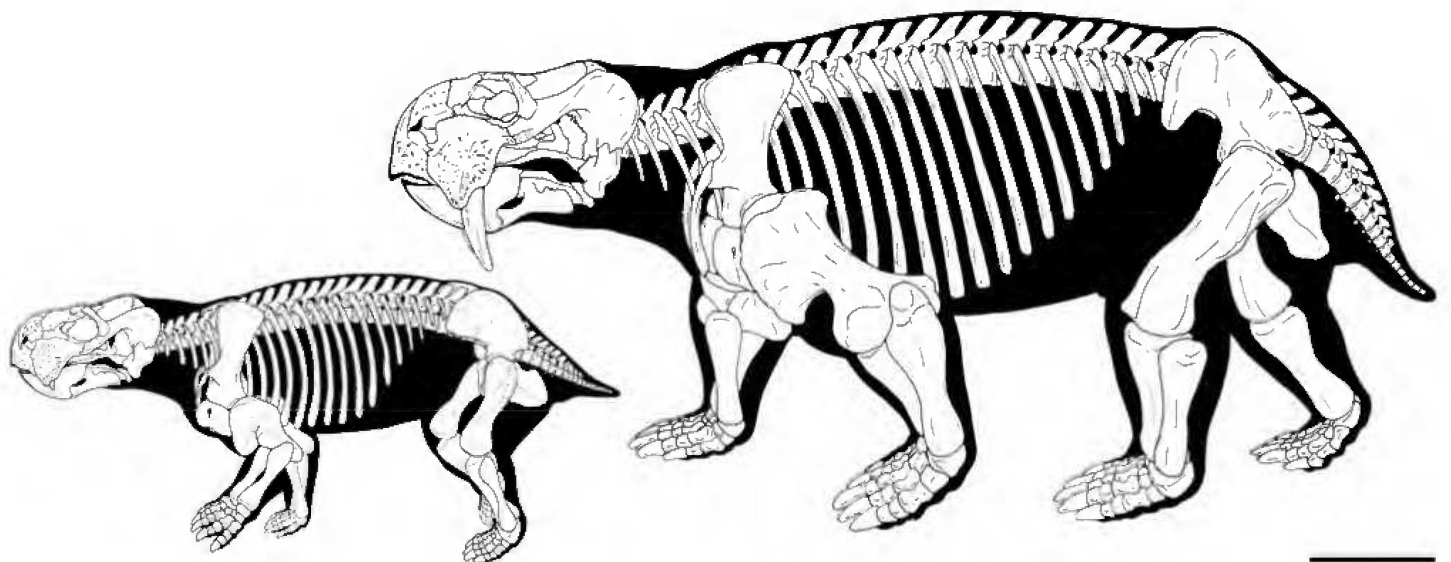

Fig.1- Skeletal reconstructions of *Dinodontosaurus*, showing the morphotypes of a juvenile (based mainly on UFRGS/PV0113T and partially on UFRGS/PV0115T) and an adult (skull based on Mata 367-99, skeleton based on UFRGS/PV0121T and modified from Cox, 1965). Scale bar = 20cm.
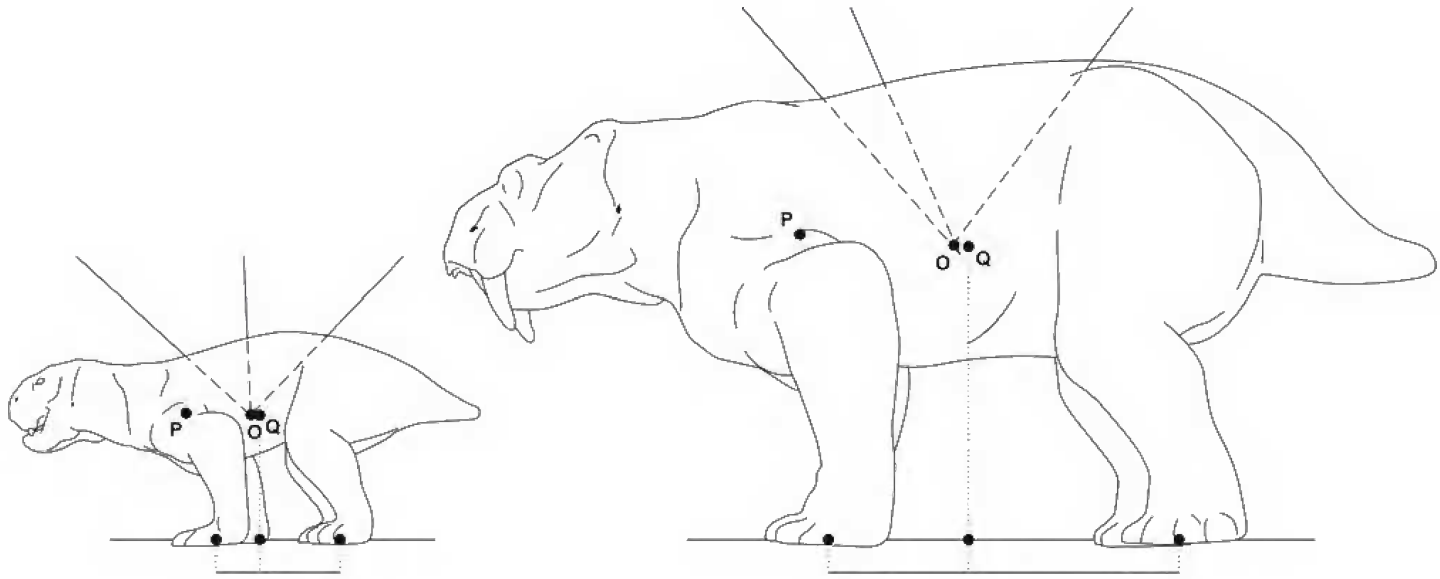
Fig.2- Location of the center of mass for juvenile and adult individuals of *Dinodontosaurus*. *O* represents the center of mass from suspension of clay models, *P* is the approximate location of lungs center of buoyance, and *Q* is the corrected location of the center of mass. In the base of the figures are the projections of the center of mass in the ground and the points of support for front and hind limbs, represented by dots, to allow the estimate of mass percentages sustained by each limb.
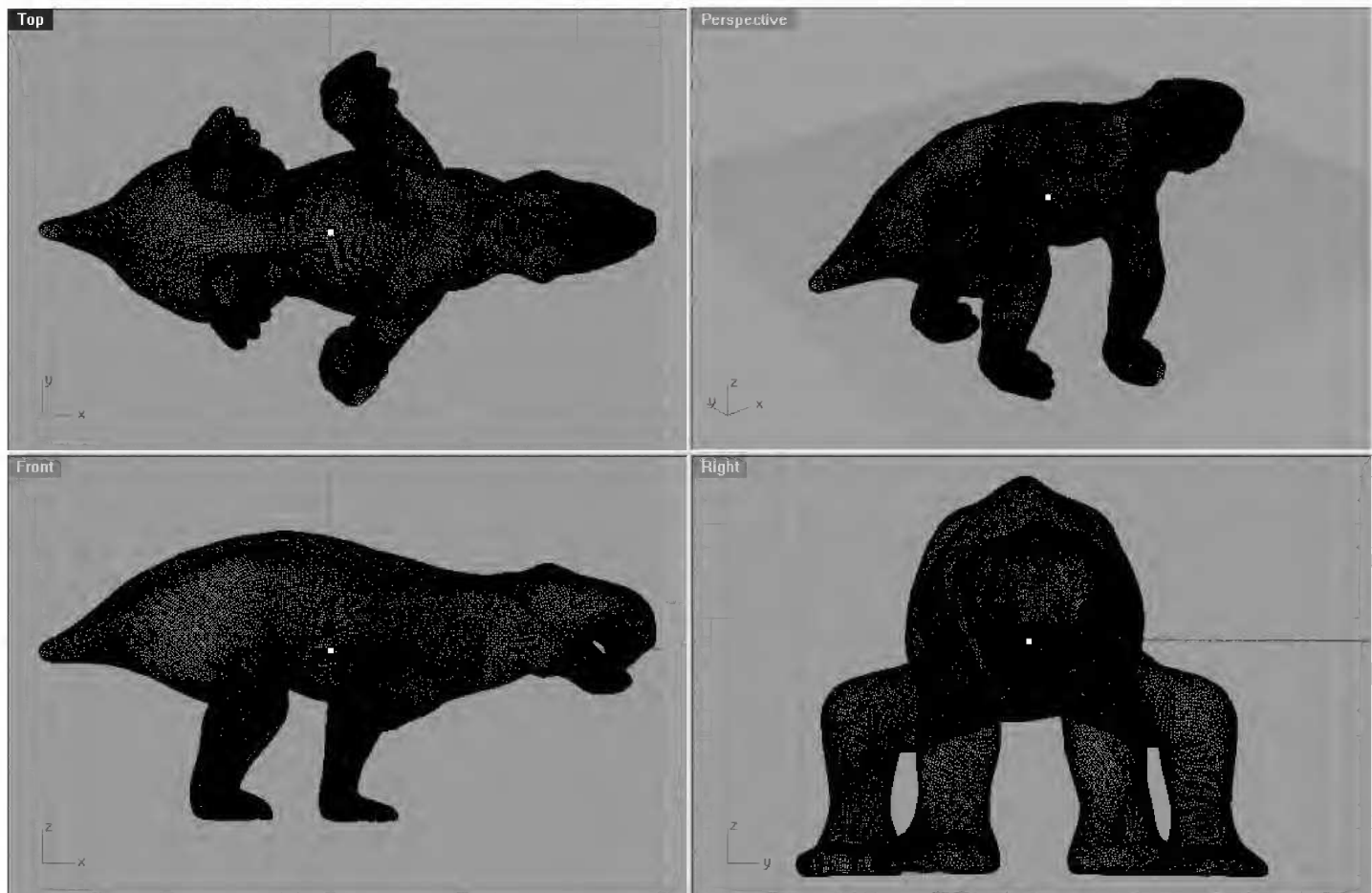

Fig.3- Screen capture image (from software Rhinoceros) of the location of the center of mass (white dot in the center of each figure) for a juvenile individual of *Dinodontosaurus*, from a digitalized model obtained with 3D-scanner.

Indicators of athletic ability for the limbs can be calculated from measurements of the transverse and sagittal diameters, as well as the length, of long bones (as the axial strength indicator, given by the expression A/amg, and the long bone strength indicator (LBSI) given by $Z/amgx$, where A is the section area, Z is the section modulus, amg is the fraction of weight supported by the respective limb, and x the half of the bone length; see ALEXANDER, 1983; 1985) (Fig.4).

The indicators of athletic ability were calculated using a solid cylinder model, not subtracting the corresponding amount occupied by the medullar channel (as made in CASINOS, 1996). This was preferred to allow comparisons with other values available in the literature, even though broken bones in the specimens allowed measuring of their walls thickness and could be possible to obtain a mean percentage of bone diameter occupied by cortex.

Some considerations must be made on the applicability of some of these indicators, once the posture and gait of dicynodonts is distinct from any living vertebrate. Even when compared with sprawling animals, there are no modern parallels for evaluations of athletic capabilities, as is usually made with such indexes (MORATO *et al.*, in press).

RESULTS AND DISCUSSION

In a general observation, the comparisons between dicynodonts and xenarthrans don't seem to proceed biomechanically, as several ground sloth taxa may have walked effectively in a bipedal gait, presenting various adaptations to facultative bipedalism. Their centers of mass are displaced caudally, being near the pelvic girdle (see, for example, BLANCO & CZERWONOGORA, 2003, for percentage of weight supported by each pair of limbs, and FARIÑA, 2001, for its relation to the center of mass). To this feature, contributes the relatively reduced skulls, anteriorly narrowed trunks, vigorous hind limbs and broad muscular tails. Besides that, the pes is normally larger than the manus, giving them a stable base while walking on two limbs. Measurements for *Megatherium* (CASINOS, 1996) revealed that the vertebrae present the height of the centra improved towards the sacrals, increasing the resistance of the vertebral column at the lumbar region, which is necessary for a bipedal stance; the hindlimb bones presented also axial strength compatible with bipedal animals, and LBSI values superior to that of the front limbs. The sloths also possess transversally expanded femora, probably in reflection of the latero-medial stresses generated by the traviportal gait.
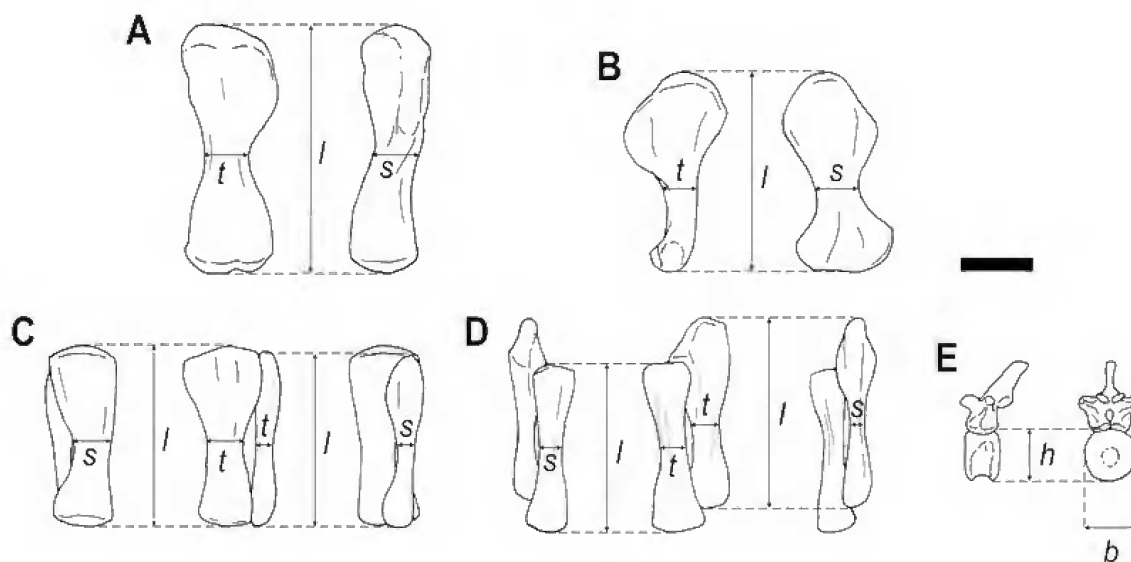

Fig.4- Key for the measurements taken from the bones of *Dinodontosaurus*: (A) left femur in dorsal and lateral views; (B) left humerus in anterior and dorsal views; (C) left tibia and fibula in medial, anterior and lateral views; (D) left radius and ulna in medial, anterior and lateral views; (E) dorsal vertebra (twentieth) in lateral and posterior views. All the long bones of the appendicular skeleton were measured for length (l), and width near midshaft, in sagittal (s) and transverse (t) diameters (in the case of the humerus, these diameters were related respectively to the antero-posterior and dorso-ventral bending stresses). Vertebrae were measured for breadth (b) and height (h) of the posterior border of their centra. Scale bar = 5cm (all drawn in the same scale).

The center of mass of *Dinodontosaurus* was located in a point in the sagittal plane about half the distance between the stylopodials, closer to the front limbs (Figs.2-3). This location was corroborated by the suspension of the sculptures as well as by the digital models. Although the center of mass have been stipulated for models composed by homogeneous matter (clay), the displacement of its position due to lungs volume would be of little significance (ALEXANDER, 1985), as it will remain closer to the forelegs. To attain a bipedal stance, any animal must adopt a posture in which the center of mass rests over or after the hindlimbs (ALEXANDER, 1985), and, in the case of *Dinodontosaurus*, such a posture would be achieved momentarily, during copula; however, the location found for its center of mass suggests that a bipedal posture would not be easily maintained without support, and a bipedal walk would be absolutely impracticable. The bipedalism in giant ground sloths is unequivocal, as it is indicated even by ichnofossils (*e.g.*, CASAMIQUELA, 1974; BLANCO & CZERWONOGORA, 2003), while the likely candidates for dicynodont's trails (*e.g.*, ELLENBERGER, 1970; HUNT *et al.*, 1993; NESBITT & ANGIELCZYK, 2002) show only quadrupedal gaits.

The estimates of the moments of resistance for the vertebral column of *Dinodontosaurus* resulted in a graphic that is also compatible with a quadrupedal animal (Fig.5), according to SLIJPER (1946). The pattern of the graphic has a lumbar peak, as well as a horizontal level near the scapular region. For *Megatherium*, the graphic presents a tapering line from the second vertebra to the end of the lumbar region (Fig.5), in keeping with a graphic for bipedal animals, except for the lack of a lumbar peak (CASINOS, 1996). This absence could be related to the xenarthrous lumbar vertebrae.
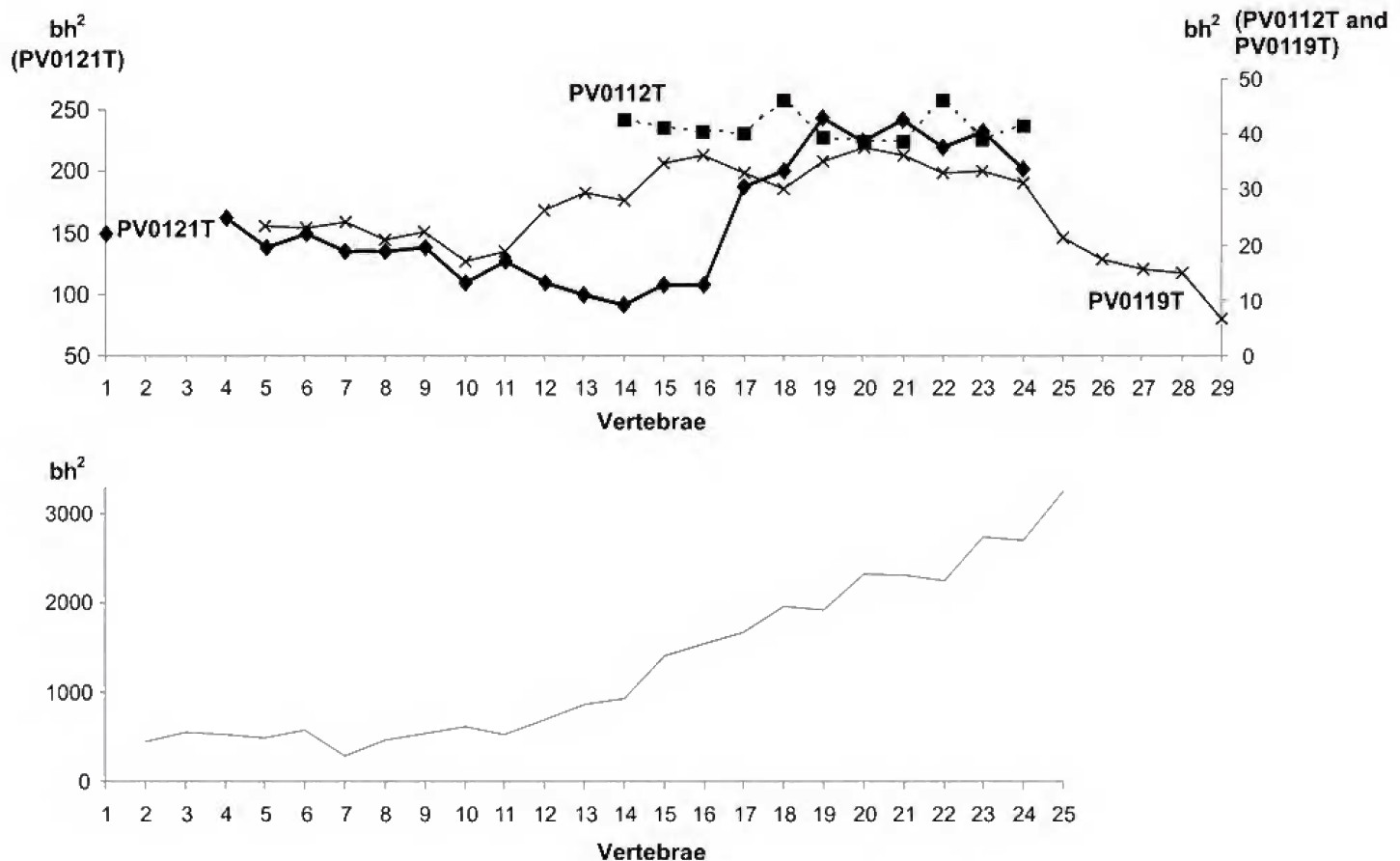

Fig.5- Moments of resistance for the different vertebrae of (above) three *Dinodontosaurus* specimens (indicated inside the graphic; UFRGS/PV0112T and UFRGS/PV0119T are juvenile individuals, while UFRGS/PV0121T is an adult), compared with (below) data for *Megatherium* (modified from CASINOS, 1996). On the *y*-axis are plotted values for the moment of resistance estimates (bh^2); on the *x*-axis, the number of the vertebrae (initiating with cervicals). In *Dinodontosaurus*, the last lumbar vertebra is number 24, and for *Megatherium*, 25.

SLIJPER (1946) already noticed that not only the vertebral centra are involved in the resistance of the column: tendons, muscles and aponeuroses also have a role in stress support, and the presence of additional zygapophyseal articulations could account for part of this support, liberating the charge over the centra. *Dinodontosaurus* does not have supplementary articulations on vertebrae, resulting in a lumbar peak in the graphic, although the zygapophyses seem well packed, and neural spines are close to each other. Also, the shallow angle that the zygapophyses made in relation to the axis of the vertebrae does not permit large amounts of dorso-ventral movement, uniformly increasing the column strength.

The axial and bending strength parameters were calculated for the long bones for anterior and posterior limbs, but first, this calculation needed body mass estimations, obtained from the models. The mass of juvenile individuals of *Dinodontosaurus* ranged from 23 to 32kg, for animals between 0.8 and 1m in length, while the adult individual could not surpass 300kg. The last value is an overestimate, as the silhouettes used are incorrect in the shape of the autopodials, caudal and cervical regions. A more likely value could reside near 250kg.

The superficial resemblance noted by CRUICKSHANK (1978) between femora of dicynodonts and ground sloths proceeds only partially, because the femur in dicynodonts is transversally expanded in the proximal end, but narrows in the midshaft, showing an elliptical section, while in sloths the transverse expansion extend all the length of the femur.

TABLE 1. Indicators of athletic ability (*A/amg* and *Z/amgx*) calculated for the limb bones of *Dinodontosaurus* (specimens identified by cataloguing numbers), compared with values for mammals (from CASINOS, 1996).

TAXON	FEMUR		TIBIA		FIBULA	
	A/amg	*Z/amgx*	*A/amg*	*Z/amgx*	*A/amg*	*Z/amgx*
Megatherium	194	42.08	742	31.40	-	-
Buffalo	-	17.74	569	21.77	-	-
PV111T	18800	164	16000	276	6990	79.4
PV112T	* 21900	* 249	-	-	-	-
PV113T	23300	259	* 12300	* 138	* 3490	25.9
PV115T	16100	146	12100	143	2580	16.5
PV116T	20700	231	-	-	-	-
PV117T	* 26100	* 315	15300	202	* 3300	* 28.0
PV118T	27500	277	14900	208	4350	37.5
PV119T	* 19200	* 204	* 14400	* 195	* 3350	* 28.2
PV120T	22100	218	-	-	-	-
PV121T	7630	73.8	5610	73.8	2380	23.4

TAXON	HUMERUS		RADIUS		ULNA	
	A/amg	*Z/amgx*	*A/amg*	*Z/amgx*	*A/amg*	*Z/amgx*
Megatherium	421	13.85	-	-	-	-
Buffalo	380	16.93	-	-	-	-
PV111T	-	-	5230	51.0	5060	39.4
PV112T	11600	139	-	-	-	-
PV113T	-	-	-	-	-	-
PV115T	* 20900	* 329	* 4660	* 49.0	* 9680	* 98.5
PV116T	14000	231	7380	91.4	6820	59.5
PV117T	-	-	3000	25.0	-	-
PV118T	25200	347	3560	29.7	* 5340	* 31.3
PV119T	10700	124	4760	40.6	6420	45.9
PV120T	10700	148	3980	37.7	5500	42.9
PV121T	7680	90.3	2080	25.8	2570	17.4

Values are given in GPa^{-1}, calculated for the direction of motion (for antero-posterior bending stresses), from measurements from bones of the left side; when this was not possible, values from the right side are given (indicated with asterisks).

This compromises the strength of the bone exactly where it is more demanded. Even then, the values obtained for the A/amg parameter, an indicator of strength in opposition to axial stresses, already show that *Dinodontosaurus* limbs were extremely resilient, even when compared with bipedal animals (see Table 1). LBSI values (the $Z/amgx$ parameter) are also much superior to values for other animals (*e.g.*, ALEXANDER, 1985, 1989; FARLOW *et al.*, 1995; and CASINOS, 1996). But it must be noted that values for humeri and femora are in the same order of magnitude, at least, which supposes a quadrupedal posture (see values for *Megatherium*: CASINOS, 1996).

Finally, it is worth to note that pes and manus of dicynodonts are all of similar dimensions, therefore the pes do not have any advantage to provide a substantial support for a continuous bipedal posture.

CONCLUDING REMARKS

The results of the present analysis suggest that, at least in what concerns *Dinodontosaurus*, there are no strong evidences to support the morphofunctional analogies with the extinct ground sloths. The comparisons made by CRUICKSHANK (1978), paraphrasing himself about previous analogies (p.122), are "tenuous to say the least". The author, for instance, discredited comparisons with modern rhinoceroses in basis of a much larger size of the latter, but if one opens space for comparisons with an extinct taxon of which there is no direct evidence of feeding behavior, why not to consider the extinct rhinocerotids or suids, whose size range varies considerably? In the other hand, there are no remarks of that matter to the much larger megatheriid sloths, some of the few sloths with extensive evidence for facultative bipedal stance to reach higher vegetation and furthermore been able to walk in this stance. Of course there won't be a perfect equivalent for dicynodont morphology, in living as in extinct mammals, but criterion for comparison cannot be ruled only by superficial and subjective observations.

There is another syllogism in CRUICKSHANK (1978) that doesn't have strong basis for argumentation. He suggests that tusks in Dicynodontia were used for display and/or threat purposes, therefore implying that tuskless forms were either nocturnal or lived in deep undergrowth. However,

the absence of tusks does not imply in absence of ornamentation, as caniniform processes in the maxillae of tuskless forms may as well have played a role in visual signaling, what may be done by several other characters present in Middle to Late Triassic tuskless dicynodonts (MORATO *et al.*, 2005). Loss of tusks could be only an apomorphic morphological differentiation (VEGA-DIAS *et al.*, 2004), and not a complete life habit indicative.

However, in order to investigate the main comparisons of Cruickshank's paper, other questions emerged. The values of LBSI found, incomparable to other animals described in the literature, can be a reflection of the demands of a differentiated posture adopted by dicynodonts, but this hypothesis still must be investigated throughout. Although these values can not be used in direct correlations with living creatures, they appear at least to be comparable with other Triassic amniotes, including non-mammalian cynodonts referred as quadrupedals (MORATO *et al.*, in press).

Some authors (including WALTER, 1986) admit that the differentiation in postures between fore and hindlimbs can imply in a differentiated functionality for the limbs, with the forelimbs more adequate for support, while the hind ones are more involved with effective thrust. Nevertheless, similar values for LBSI of fore and hind members can indicate that they were both effectively utilized in the locomotion, and, although they had dynamically distinct motions, they were subject to similar bending stresses; by other hand, the extreme bone strength can mask a sum of locomotory and body-support stresses, due to the arrangement of the limbs itself.

ACKNOWLEDGEMENTS

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